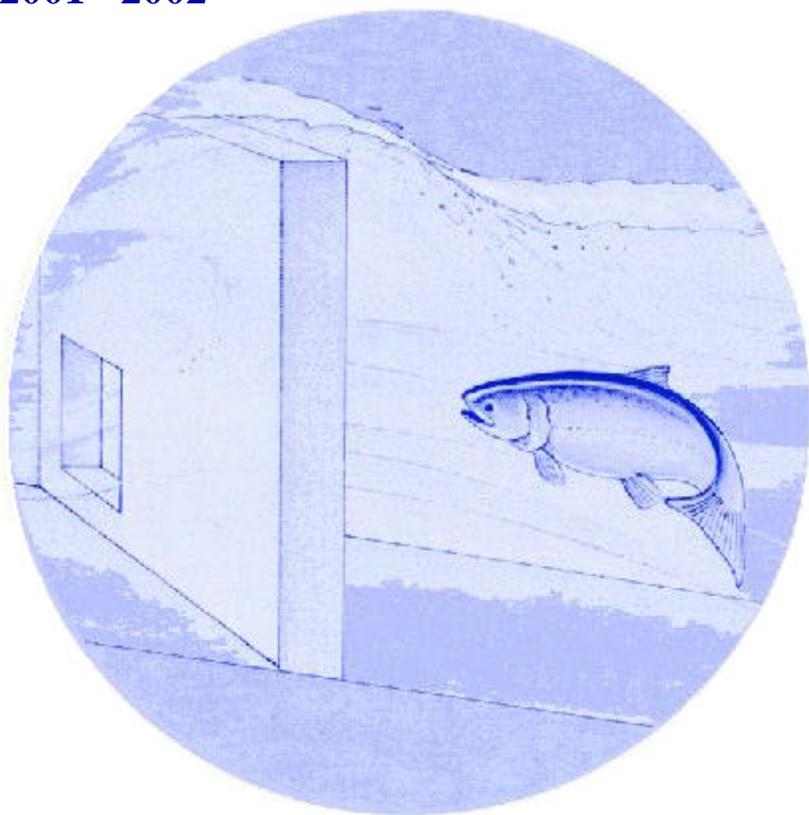


Comparing the Reproductive Success of Yakima River Hatchery and Wild-Origin Spring Chinook

Yakima/Klickitat Fisheries Project Monitoring and Evaluation

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Comparing The Reproductive Success Of Yakima River Hatchery- And Wild-Origin Spring Chinook

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SUMMARY

In 2001 hatchery- and wild-origin spring chinook were placed into an observation stream located at the Cle Elum Supplementation Research Facility to compare their reproductive success. Two groups containing both wild- and hatchery fish of both sexes were brought into the stream and allowed to spawn. Their longevity, spawning participation, and reproductive success were assessed. In addition, wild- and hatchery-origin precocious males were also introduced into one of the sections and allowed to spawn. We found that hatchery and wild males generally lived longer than females. In one group hatchery and wild females lived for similar periods of time while in the other wild females lived longer than hatchery fish. Wild females were also more successful at burying their eggs and the eggs they buried had higher survival rates. This result occurred in both groups of fish. Spawning participation in males was estimated by using two statistics referred to as percent gonad depletion (PGD) and percent testes retention (PRT). Both of these measures assumed that loss of testes weight in males would reflect their spawning participation and therefore could be used to estimate reproductive success. Hatchery and wild males had similar PGD and PRT values. One of these measures, PRT, was negatively associated with male reproductive success, confirming the idea that reduction in testes weight can be used as a surrogate measure of a male's ability to produce offspring

Fry from the observation stream were collected throughout the emergence period that ran from January through May. Proportionate sub-samples of these fish were removed and microsatellite DNA was extracted from them. Pedigree analyses were performed to ascertain which adult fish had produced them. These analyses disclosed that wild males were more successful at producing progeny in one of the groups. No difference occurred in the other group. Precocious males and jacks fathered fewer progeny than did fish maturing at ages 4 and 5. In addition, male reproductive success was more than twice as variable as that seen in females. Some males apparently never spawned and others produced more than 7,000 offspring an amount that was more than double the quantity generated by the most successful female. Behavioral observations showed that a number of factors besides male origin influenced their reproductive success. One was relative body size; larger males tended to dominate smaller opponents and therefore had greater access to females. However, male dominance was not always related to relative size. The ability to attack and chase opponents was, however, positively related to reproductive success. We also discovered that the reproductive status of females and the social status of males were often reflected by their nuptial coloration. Territorial females typically had a single broad purple black stripe, light green or brown backs and white or gray ventral surfaces. Dominate males on the other hand, were generally a uniform dark brown or black color. The percentage of time that a male possessed a dark color pattern was positively linked to his reproductive success, as was the percentage of time he was observed courting or defending a female. The number of times a male was chased or attacked by a female also affected his reproductive success, in this situation the greater the frequency of such attacks the lower the reproductive success of the male. The pedigree analyses also disclosed that both hatchery and wild precocious males were able to fertilize eggs and produce offspring under natural spawning conditions.

In conclusion we found differences in the reproductive competency of hatchery- and wild origin spring chinook. Wild females were better at depositing their eggs and having those eggs produce fry. In one study group wild males were more successful at producing offspring than hatchery males. Additional replications of such evaluations are being carried out to determine if the differences seen can be replicated. A repeat of the work done in 2001, for example, was performed in 2002 and additional studies will take place this coming year.

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INTRODUCTION

Background

The Yakama Indian Nation and the Washington Department of Fish and Wildlife began a spring chinook supplementation program in the upper Yakima River in 1997. Every year since then, adult spring chinook native to the upper Yakima have been captured and held at the Cle Elum Supplementation Research Facility (CESRF). At maturation these fish are spawned, and their offspring are incubated for six months and reared at the CESRF for an additional nine to ten months. The juveniles are then transferred to three acclimation sites located in the upper Yakima basin where they are reared for another month or longer before being allowed to voluntarily enter the river. The acclimation sites were established to disperse returning hatchery-origin adults throughout the upper basin. It was hypothesized that fish rearing in each acclimation site would imprint on their final rearing waters and thus have a proclivity to return to this portion of the basin once they reached maturity. In 2000, the first three-year old adults (jacks) produced by the hatchery program returned to the Yakima River, and in 2001 both three- and four-old hatchery-origin adults were present. Every fish produced by the supplementation program receives marks and tags so that they can be identified at the adult stage. These fish are not used as broodstock, instead they are allowed to migrate into the upper Yakima and reproduce under natural conditions.

A growing body of literature, however, suggests that adult salmon produced by artificial culture are not as reproductively successful as wild fish when they spawn under natural conditions. Behavioral, morphological, and physiological divergences have been observed between wild- and hatchery-origin fish (Table 1, *see* Fleming and Petersson 2001 and Schroder et al. 2003 for more comprehensive reviews). These disparities are the likely proximate causes of the differences seen in the reproductive success of hatchery and wild salmonids. Two evolutionary paradigms have been proposed to explain why salmonids cultured in hatcheries are altered genetically and phenotypically from wild-origin cohorts. The first proposes that natural selection has been significantly relaxed in hatcheries. Consequently, fish that normally would have perished because of the possession of unsuitable traits are able to survive. If these traits have a genetic basis they can become established in a hatchery population and cause its productivity to be less than expected if hatchery fish are once again exposed to natural selection pressures. The second theorizes that environmental and social conditions in hatcheries are much less variable than the natural environment and that these conditions will remain relatively constant from one generation to the next. In this circumstance, selection for genetic traits that adapt fish to artificial culture will become prevalent in the population. Many such traits are likely to be mal-adaptive under natural conditions. For example, Heath et al. (2003) document cases where egg sizes in salmonid populations have dramatically decreased in cultured populations apparently due to an increase in fecundity. Such a response could be an outcome of relaxation for large eggs or a directed selection toward more eggs. No matter what its origin, their examples illustrate that unintentional selection in hatcheries can lead to significant changes in traits that are directly linked to survival under natural conditions (Heath et al. 2003).

Table 1. A summary of some of the behavioral, morphological, and physiological differences observed between hatchery- and wild-origin salmonids.

Trait	Hatchery Females Vs. Wild Females	Hatchery Males Vs. Wild Males
Reproductive Behavior	Poorer at acquiring territories Build fewer nests Less successful at egg burial Poorer at guarding nests	Less aggressive Spend less time searching for females Lower frequency of courting behavior Less attentive to females
Morphology At Maturation	Less pronounced secondary sexual characters e.g., smaller kypes Less fusiform	Shorter kypes Smaller jaws and adipose fins Less fusiform
Physiological Differences	Delayed and accelerated maturation timing Increases and decreases in egg size and fecundity Lower cardiac/somatic index values	Increase in gonad size Lower cardiac/somatic index values

How artificial culture affects salmonids appears to be influenced by three factors. First, the longer individual fish are held in culture the greater the likelihood they will experience genetic change (e.g., domestication), or have their individual behaviors altered by the hatchery environment. Thus, salmonids like steelhead, coho, and spring chinook that typically experience prolonged rearing periods in hatcheries are expected to be more susceptible to domestication and more likely to express mal-adaptive behaviors than species that have shorter tenures in a hatchery environment. Second, the more generations a population is subjected to a hatchery environment the greater the risk that domestication effects will accumulate and manifest themselves. And third, the impact of hatchery life on naturally spawning hatchery fish is not equivalent across sexes. Naturally spawning hatchery-origin males typically express a greater deficit in breeding success than hatchery-origin females (Table 2).

Table 2. A summary of the differences found in the reproductive success of hatchery- and wild-origin salmonids spawning under natural conditions.

Species	Generations In Culture	Sex	Relative Efficiency (Hatchery Vs. Wild)	Citation
Coho	4 to 5	Male Female	47 to 62% 82 to 88%	Fleming and Gross 1993
Atlantic Salmon	1	Male Female	65% 82%	Jonsson and Fleming 1993
Atlantic Salmon	1	Male Female	51% No Difference	Fleming et al 1997
Atlantic Salmon	5	Male Female	1 to 3% 20 to 40%	Fleming et al. 1996
Atlantic Salmon	5	Male Female	24% 32%	Fleming et al. 2000

The Yakima River spring chinook supplementation project limits inadvertent genetic change and domestication by continuously choosing wild-origin adults as broodstock. Consequently, all adults produced by the hatchery, other than a few selected for research purposes, will naturally reproduce in the upper Yakima River basin. It was hypothesized that this strategy would reduce any accumulation of deleterious genetic changes caused by being incubated and reared in the CESRF and its acclimation sites. However, alterations in the behavior, morphology, and physiology of cultured fish can also be induced by environmental conditions experienced during juvenile life. Again, efforts were made to ameliorate some of these effects. The fish are reared using relatively low densities, and half are raised in environments possessing underwater feeders, floating covers, suspended in-water structure, and painted raceways. Moreover, an attempt was made to feed all the fish in a manner that would mimic the growth patterns of spring chinook rearing in the Yakima River. Nonetheless, certain features of hatchery culture cannot be easily alleviated. Artificial spawning precludes mate choice and the expression of important reproductive behaviors; concrete raceways possess restricted flow regimes; commercial diets are uniform in shape, color, and are passive particles as opposed to moving targets; and even low-end rearing densities in hatcheries are much higher than those experienced under natural conditions. Consequently, fish reared in these kinds of environments may express different phenotypic attributes at maturity than those produced under natural conditions. Table 2 illustrates that such differences can be biologically important since researchers have found that exposure to hatchery conditions for even a single generation will impact the reproductive competence of salmonids when they spawn under natural conditions.

One of the objectives of the Yakima Fisheries Project evaluation program is to determine whether the adults produced from the Upper Yakima spring chinook supplementation program have experienced any reduction in their capacity to reproduce under natural conditions. To accomplish that objective, an observation stream was built in 2000 on the grounds of the CESRF. Wild- and hatchery-origin spring chinook adults were introduced into the stream in September of 2001 and allowed to reproduce in the stream. In this document we describe the results of comparisons that were made between: 1) the body sizes of the hatchery and wild chinook placed into the stream; 2) how long fish of each type lived after being introduced into the stream; 3) the spawning participation or capacity of wild and hatchery fish to express their gametes, and 4) the ability of each type of adult to produce fry. The latter analyses were made possible by performing pedigree assessments on randomly sampled fry. The results of these microsatellite DNA based examinations showed that some males produced large numbers of fry while others apparently never spawned. In an effort to understand the source of this variation we evaluated whether linkages existed between male behavior and the production of offspring. These assessments were made on a set of wild-origin males that had been placed into the observation stream in 2000. Like the males introduced into the observation stream in 2001, they also exhibited a high degree of variation in their reproductive success. These fish were chosen for this analysis because the extensive behavioral observations made on them have been completely analyzed. Similar observations made on the hatchery and wild males fish placed into the observation stream

in 2001 are still undergoing analysis. All results presented in this report should be considered preliminary until they are published in the peer-reviewed literature.

METHODS

Observation Stream

The observation stream located on the grounds of the CESRF is 127 m long by 7.9 m wide and has a “U-shaped” footprint. It is subdivided by eight concrete cross weirs into seven subsections, a curved section or elbow that is 21.m long by 7.9 m wide and six straight sections each measuring 15.2 m long by 7.9 m wide. The stream has banks with 2:1 slopes that are armored with large river rock (10 to 30 cm in diameter) and when it is in operation its wetted width ranges between 4.3 to 5.5 m. The streambed is lined with geotextile to prevent water loss and is filled with 90 cm of double washed stream gravel that ranges in size from 7.1 mm (0.28 inches) to 100 mm (3.9 inches) in diameter. When the gravel was first placed into the stream in August of 2000 it had a Fredle Index (Lotspeich and Everest 1981) value of 10.6. The stream’s water supply is the discharge water from the 18 raceways located at the CESRF. Water from the raceways is pumped into the stream from September through May by using up to four, 25 hp electric pumps and a gate valve regulates flow. Enough water is pumped into the stream to produce velocities that are ≥ 0.1 m/sec but less than 1.5 m/sec. In addition, an attempt was made to keep water depths \geq to 0.1 m by using stop logs placed in the cross weirs. These criteria were patterned after the velocities and depths that naturally spawning chinook have been observed to use (Healey 1991; Bjornn and Reiser 1991). Velocity and depth measurements were made at 775 points in the stream in 2001 to determine the proportion of the structure that met these requirements. In addition, Tidbit temperature loggers were placed in the observation stream and they recorded water temperatures once every 15 minutes during the spawning and incubation periods.

To facilitate fish observations, a 2.1 m tall observation wall was installed on both banks of the stream. The wall was built by attaching camouflage netting to three-meter tall fence posts set on 2.4 m centers. Top and bottom rails were attached to the fence posts to help support the camouflage netting. Openings, at eye level, were cut into the netting every 2 meters along its length. Observations made on naturally spawning wild spring chinook in the upper Yakima River showed that both males and females made extensive movements on their spawning grounds. To provide the fish with the opportunity to express this type of behavior we subdivided the observation stream into two equal parts referred to as the upper and lower portions of the stream. Each portion consisted of three of the straight sections that measured 15.2 m long by 7.9 m wide and therefore was 45.6 m long by 7.9 m wide. Every 15.2 by 7.9 m section had a grid system made of 0.6 cm nylon cord that was stretched approximately 30 cm over the surface of the water. The squares in the grid measured 1.5 m wide by 3 m long and each was provided with a unique alphanumeric designation so that fish movements and locations could be recorded. In addition, each of the seven subsections was named. The three uppermost straight sections were called 1-1, 1-2, and 1-3; the curved section was referred to as the elbow

while the bottom three sections were identified as sections 2-1, 2-2, and 2-3. A more detailed description of the observation stream can be found in Schroder et al. (2003).

Selection of Hatchery- and Wild-Origin Adults

Spring chinook returning to the upper Yakima River from April through August are randomly selected at the Roza Adult Monitoring Facility and transported to the CESRF where they are held in 30.5 m long by 4.6 m wide by 3 m deep ponds. Beginning in early September the fish are inspected once a week to assess their maturity. Mature fish destined for the observation stream are captured by dip net and anesthetized in a 1:19,000 part solution of MS222 (Bell 1964). Once docile, the fish are weighed to the nearest gram, have fork lengths taken to the nearest mm, and are tagged with numbered 3.8 cm in diameter Petersen Disks. DNA samples are also taken by removing a small amount of fin material from the trailing posterior corner of the dorsal fin. These samples are placed in 100% ethanol and transported to WDFW's genetic lab for microsatellite DNA extraction and characterization. After being tagged, one or two individuals were placed into an insulated 124 L capacity cooler and transported to the observation stream. The entire process from anesthetization to fish liberation into the observation stream took slightly longer than 3 minutes per fish. All the fish placed into a section of the stream were tagged and liberated on the same day; this process usually took three hours or less to complete.

Comparisons Between Hatchery- and Wild-Origin Adults

Body Size Comparisons

Two, One-Way ANOVAs were performed to determine if size differences existed among the hatchery- and wild-origin males and females placed into the observation stream. One was run on the body weights of the fish that were placed into the upper part of the stream that consisted of sections 1-1, 1-2, and 1-3 and the second was performed using the weights of the fish introduced into the lower portion containing sections 2-1, 2-2, and 2-3.

Longevity Evaluations

The length of time individual fish lived after they were introduced into the observation stream was assessed by periodically inspecting the stream for recently dead fish. Usually the sections were monitored three or more times during daylight hours and once close to dawn to assess which fish had died during the night. How long a fish lived in the observation stream was determined by subtracting the average time fish entered its section from the date and time of its death. For example, adult chinook were placed into the upper-portion of the observation stream (sections 1-1,2, and 3) on September 12, 2001 from 8:30 to 10:30 AM and had a mean entrance time of 9:38 AM. If an individual was found dead on September 14 at 9:38 AM it was considered to have a longevity value of 48 hours. Because the time of death information obtained on individual fish could be off by as much as 8 hrs (e.g., for fish collected at dawn) the longevity data were

considered to be ordinal in nature. Consequently, non-parametric tests were used to see if hatchery- and wild- origin individuals of the same sex placed into the same section lived for differing periods of time. Nonparametric tests were also performed to see males and females lived for differing amounts time in the same portion of the observation stream.

Spawning Participation

Spawning participation or the apparent capacity to express gametes was estimated for each individual placed into the observation stream. The procedures used for each sex were somewhat different. Female spawning participation was estimated by dividing her actual egg deposition (AED) by her potential egg deposition minus any eggs lost at tagging. To develop such an estimate the fecundity or PED of each female had to be predicted. This was accomplished by using a multiple regression formula generated from the four-year-old females that had been artificially spawned at CESRF in 2001. In this regression, fecundity was the dependent variable while female weight and egg weight were independent variables. The AED value of each female was partially determined by ascertaining the number of eggs each female had retained at death. Misshapen eggs or those that were still firmly attached to the ovarian membrane were not counted. This value was then subtracted from the predicted fecundity for that female to produce an AED estimate. During the tagging process a few females expelled eggs and these were hand-counted and subtracted from the PED value for that female; producing an adjusted PED. The AED value of each female was then divided by its PED or when necessary by an adjusted PED value to obtain a percent spawned or spawning participation estimate. Thus, spawning participation values represented the percentage of the potential eggs females brought into the observation stream that were actually deposited. AED values on the other hand, represented an estimate of the absolute number of eggs females were able to deposit in their nests.

Chi-square tests were used to determine if hatchery- and wild-origin females differed in their ability to deposit their eggs. In addition, linear regressions between female body weight and arcsine transformed percent spawned values (Zar 1999) were performed to determine if female size and spawning success were related to one another in hatchery- and wild-origin females. Moreover, isotonic regressions were employed to explore whether the length of time hatchery- and wild-origin females lived affected how completely they were able to spawn. Isotonic regression relaxes the assumptions of linear regression and tests whether a consistent increase (or decrease) in the dependent variable, Y (percent spawned), is a function of the rank order of the values of an independent variable, X or in these tests hours alive in the observation stream (Sokal and Rohlf 1995). Four such regressions were done, one for each type of female placed into the upper and lower portions of the observation stream.

Two different approaches were used to estimate the spawning participation of males. Both relied on three assumptions. First, that a relatively consistent percent of an unspawned male's weight was made up of testes, second, hatchery- and wild-origin males have similar body weight/gonad weight relationships, and three that weight loss in testes is directly linked to the number of times a male spawns. Earlier work on upper Yakima

spring chinook illustrated that a positive relationship exists between male body weight and testes weight in four-year-old males (Schroder et al. 2003). An analysis of covariance was performed to evaluate whether hatchery- and wild males have similar relationships between their body weights and gonad masses. Finally, a study that examined the association between weight loss in testes and the number of times male chum salmon were artificially spawned supports the expectation that a positive correlation between spawning frequency and testes depletion occurs in semelparous salmonids (Schroder 1973). Based upon this evidence we developed two indices of male spawning participation. One is referred to as percent gonad depletion (PGD) while the other is called percent retained testes weight at death (PRT).

To generate percent gonad depletion or PGD values, the testes weight for each male placed into the observation stream was estimated by using the following linear regression formula from Schroder et al. (2003): Un-spawned Testes Weight = $31.5 + ((0.043)(\text{male body weight in grams}))$. The independent value was male body weight while the dependent value was testes weight in un-spawned four-year-old upper Yakima spring chinook. Similar formulas for jacks (three-year-old males) and five-year-old males have not yet been developed because not enough data have been gathered on un-spawned males possessing those life histories. Consequently, estimates of un-spawned testes weights of such males were not made since they may well possess different body weight/gonad weight relationships than four-year old fish. However, it was still possible to compare PGD values between hatchery- and wild fish because most of the males placed into the observation stream in 2001 were four-year-old fish.

After a male died its testes were carefully removed from the coelomic cavity by severing the mesenteries that attached it to the transverse septum and air bladder. The removed testes were then weighed to the nearest tenth of a gram. Percent gonad depletion or PGD values were calculated by dividing testes weight at death by the testes weight predicted to occur prior to spawning. The other estimate of male spawning participation, percent testes weight retained, also used the weight of a male's testes at death. In this case, the value is divided by a male's body weight at the time he was introduced into observation stream. The resulting quotient represents the percentage of a male's weight comprised of retained testes (PRT). We believe that this percentage can be used to estimate the spawning participation because males appear to allot similar proportions of their body weights into gonadal material. Consequently, males that have repeatedly spawned will possess smaller PRT values at death than those that were not as active.

A total of four Mann-Whitney U tests (Zar 1999) were used to compare male spawning participation. One evaluated whether PGD values in hatchery- and wild-males placed in the upper section of the observation stream differed from one another. A similar test examined this relationship in the males placed in the lower portion of the stream. PRT values obtained from hatchery- and wild-origin males spawning in the upper and lower portions of the observation stream were examined in the same manner. In addition, linear regression analyses were used to examine how body weight affected their PGD and PRT values.

Assessing Reproductive Success

The reproductive success of each adult fish placed into the observation stream was estimated by performing a pedigree analysis based on microsatellite DNA. This analysis matched the genotypes of prospective parents to those that existed on putative offspring. As indicated above, samples of microsatellite DNA were collected on every adult fish placed into the observation stream. DNA samples were also collected on a randomly selected proportion of the fry that emerged from the observation stream. These were obtained by placing fyke nets with attached live boxes at ends of the upper and lower portions of the stream. The traps were installed in mid-January, several weeks prior to fry emergence to ensure that a representative sample was acquired. The live boxes were checked daily, captured fry were counted, and a sample was taken by randomly removing ten percent of the fry and placing them in pure ethanol. This procedure was continued until fry emergence ceased, at that time the upper and lower portions of the stream were seined and electro-shocked so that fry rearing in the channel could be counted and sampled. Our goal was to obtain a sample of 1000 fry from each portion of the observation stream. More than this number were collected; therefore the number of fry analyzed from each day's sample was reduced by a consistent percent to produce a 1000 fry sample for each portion of the observation stream. This simple approach meant that the number of fry analyzed for a given day was proportionate to the number of fry captured on that date.

Standard microsatellite DNA methods were employed to determine the genotypes of the parent fish and fry. Template DNA was extracted from whole fry and adult tissues by using chelex resin and microsatellite DNA was selectively amplified by using the polymerase chain reaction. Microsatellite alleles were run on an automated sequencer (ABI 3730) and genotypes were assessed using GENEMAPPER software. CERVUS software was used to assign the sampled fry to the adults placed into the stream (Sewall Young personal communication).

A series of chi-square tests were performed to evaluate differences in the capacity of hatchery- and wild-origin parents to produce fry. Two were directed toward comparing hatchery- and wild females. The first evaluated whether a difference existed in the ability of females of different origins to convert their PEDs (potentially deposited eggs) to fry while the second asked whether female origin affected the ability of deposited eggs (AEDs) to survive to fry. Another set of Chi square tests evaluated whether hatchery- or wild-males produced more offspring than would be expected under random mating. Chi square tests were also used to determine if hatchery and wild fish preferred to mate with partners having the same or different treatment origins than themselves. The null hypothesis in these tests was that who mated with whom was not affected by the origin of the interacting fish. In addition, linear regression analyses were performed that examined the relationships between male PGD and PRT values and the ability to produce fry to see if these estimates of male spawning participation were related to offspring production. Regression analyses were also used to assess the importance of male body size on the ability to produce fry.

The relationship between male reproductive behavior and the production of fry. Scan and focused behavioral observations (*see* Schroder et al. 2003 for more details) were made on the adults while females prepared nests and spawned. During these observations the location, color pattern, reproductive status, and frequency of a suite of courtship and agonistic behaviors were recorded on the fish being watched. These data were used to see if the color patterns present on adult fish could be linked to their social status (males) or reproductive condition (females). In addition, the affect of male dominance and the role that female aggression on potential male partners had on the reproductive success of males was evaluated by using correlation and regression methods. These latter tests were done on behavioral data collected from wild spring chinook spawning in the observation stream in 2000. Scan and focused observations were made on hatchery- and wild fish spawning in the stream in 2001 but they have not yet been completely analyzed.

RESULTS

Environmental Conditions In the Observation Stream

Gravel Composition

Five or more gravel samples were collected from each 15.2 m by 7.9 m wide section of the observation stream by using a McNeil sampler. Samples were taken in early September prior to adult introduction in 2001 and again after fry emergence had been completed in the spring of 2002. Gravimetric analyses on the samples allowed us to: 1) compute the geometric mean of the gravel particle size (D_g) for each sample; 2) determine the percentage of material in each sample that was less than or equal to 2 mm in diameter (“fines”); and calculate a Fredle Index value for every sample. Table 3 shows the results of these assessments on the gravel samples that were collected just prior to adult introduction in 2001. The samples collected after fry emergence in 2002 are currently being analyzed.

In general, egg-to-fry survival increases as D_g values rise and percent fines decrease (Chapman 1988). Lotspeich and Everest (1981) however, demonstrated that gravel with similar D_g values can have differing amounts of fines, pore size distributions and permeability values. Consequently, to take these factors into account they developed the Fredle index that equals the D_g value of a gravel sample divided by its gravel sorting index or S_o value (Krumbein and Pettijohn 1938). Gravels possessing Fredle index values greater than 5 appear to provide optimal egg incubation conditions for salmonids (Lotspeich and Everest 1981; Chapman 1988). As table 3 illustrates the observation stream possessed a gravel mixture with a mean Fredle index value of 7.6 at the time adult fish were introduced in 2001. The waters that supply the stream can carry sand and organic material into the stream and thus the Fredle value from the fall of 2001 may have decreased over the incubation period. For example, Schroder et al. (2003) showed that the Fredle index values in the observation stream were reduced from a mean of 10.6 to one of 7.6 during the 2000 – 01 spawning and incubation period. Whether a similar decrease occurred during the 2001-02 period will remain unknown until analyses of the gravel samples collected in 2002 have been completed. Even if a similar absolute drop

occurred, the gravel composition in the stream would still remain close to optimal for incubating salmonids (Chapman 1988).

Table 3. The geometric mean particle size, percent fines, and Fredle Index values obtained from gravel samples removed from the observation stream in August 2001.

Stream Section	No. Of Observations	Geometric Mean (D_g) Of Particle Sizes	% Of Particles < 2 mm	Fredle Index Value
1-1	7	15.0	1.37%	8.0
1-2	5	14.5	1.12%	7.0
1-3	5	14.8	1.42%	8.4
2-1	6	14.2	0.82%	7.8
2-2	7	13.1	0.71%	7.2
2-3	6	12.8	0.97%	7.3
Overall Mean		14.1	1.07%	7.6

Water Velocity, Volume, Depth, And Temperature In The Observation Stream

Healey (1991) and Bjornn and Reiser (1991) summarized the water depth and velocity values that spawning spring chinook prefer for their redd locations. Healey's review indicated that chinook have spawned in waters as shallow as 10 cm whereas Bjornn and Reiser report that depths equal to or greater than 30 cm are chosen. Preferred velocities ranged from 10 cm to 150 cm per sec in Healey's review, whereas Bjornn and Reiser found that spawning occurred in areas with water velocities ranging from 30 to 90 cm per second. We collected water velocity and depth data from 56 transects that were located every 1.5 m down the length of the stream. Individual depth and velocity measurements were taken at 30 cm intervals along each transect. Depending upon the width of the stream, 13 to 18 points were measured in each transect. These measurements were taken to help characterize the general flow patterns in the observation stream and to estimate how much of it possessed velocities and water depths preferred by spawning spring chinook. As Table 4 illustrates 37 to 76 % of the points measured had desired velocities and 70 to 90% had appropriate depths.

In a previous report, Schroder et al. 2003 the general water flow and velocity conditions present in the stream were described. Water movements similar to those previously reported occurred in 2001. In general, velocities were highest just downstream of the concrete cross weirs. This happened because each weir has a 60 cm mid piece that prevents water from moving evenly from one section to the next. Instead, upstream water is slightly constrained and forced to move through two 1.8 m wide slots before entering an adjacent downstream section. Because of this discharge pattern two almost equal thalwegs are created at the anterior end of each 15.2 m by 7.9 m section. As water moves downstream the thalwegs tend to commingle with one another and velocities decrease as water moves downstream. Consequently, the observation stream possessed zones with

high flows (> 1.6 m/sec), areas with back eddies and also places with no apparent water velocity. Such an environment provided adult females with opportunities to select and compete for portions of the stream with desirable water velocities and depths

Table 4. Water velocity, depth, and flow observed in the observation stream during the 2001 spawning period.

Stream Section	No. Of Obs. Points	Pts With Velocities From 10 cm –1.5 m/sec	Pts With Velocities From 30 – 90 cm/sec	Depths > 10 cm	Depths > 30 cm	Flow m ³
1-1	128	119	53	125	92	0.39
1-2	145	104	36	141	120	0.39
1-3	133	90	53	129	82	0.38
2-1	129	101	55	127	81	0.39
2-2	116	79	55	115	87	0.40
2-3	124	95	31	123	89	0.35
Totals	775	588	283	760	551	
% Of Points		75.9%	36.5%	98.1%	71.1%	

The water temperatures experienced by the adult fish placed into the upper and lower sections of the observation stream were initially different from one another. Fish introduced into the upper section on September 12, spawned in relatively warm (16.1 to 17.1° C) water while those introduced into the lower section on September 19, reproduced when water temperatures ranged from 13.9 to 14.4° C. From September 12 until early December water temperatures steadily dropped until they reached 2 to 3° C where they remained until mid-February. From this point on temperatures generally increased until they reached a little over 9° C in mid April. Water temperature in the stream remained at that level until the fry migration period ended in late May.

Comparisons Between The Hatchery- and Wild-Origin Spring Chinook Placed Into the Observation Stream

Biological Traits Of The Spring Chinook Placed Into The Observation Stream

On September 12, 2001 twenty-one females (10 hatchery- and 11 wild-origin), twenty-two males (11 hatchery- and 12 wild-origin) and three jacks (2 wild and 1 hatchery) were introduced into the upper section of the observation stream. A week later, fifty additional spring chinook were placed into the lower portion of the observation stream. In this instance, twenty females (10 of each type), seventeen males (7 hatchery- and 10 wild-origin), two hatchery- and one wild-origin jack, and ten precocious males (5 hatchery- and 5 wild-origin) were released. Precocious spring chinook reach maturation without making an anadromous migration and in the Yakima River most mature at ages 0+ or 1+ although some may mature as 2+ fish. All of the hatchery precocious males placed into the observation stream were 1+ fish that had been obtained from the acclimation ponds. After being removed from an acclimation pond they were transported back to the CESRF

and held until being placed into the observation stream. The wild precocious males were all 0+ individuals collected from the upper Yakima River. They were also held at the CESRF until being released into the observation stream. The ages, size, origin, tag numbers, estimated fecundities and testes weights of the fish placed into the observation stream in 2001 are shown in Table 5.

Table 5. Biological traits of the hatchery- and wild-origin spring chinook placed into the observation stream in 2001.

Hatchery- and Wild Origin Females: Upper Portion (Sections 1-1, 1-2, & 1-3)							
Date Introduced To Stream	Type ¹	Age	Tag No.	Weight (Kilos)	Fork Length	Est. Fecundity ²	Eggs Lost At Tagging
12 Sep 01	HF	4	YY00	3.074	651	3358	0
12 Sep 01	HF	4	YY03	3.916	720	3739	0
12 Sep 01	HF	4	YY04	4.062	729	4084	0
12 Sep 01	HF	4	YY05	5.377	760	6156	8
12 Sep 01	HF	4	YY08	4.403	752	5052	1
12 Sep 01	HF	4	YY13	4.377	754	4492	0
12 Sep 01	HF	4	YY15	4.141	731	3848	0
12 Sep 01	HF	4	YY16	4.435	745	4599	0
12 Sep 01	HF	4	YY17	4.763	754	4714	0
12 Sep 01	HF	4	YY20	3.962	714	4219	0
12 Sep 01	HF	4	YY24	3.546	695	3600	0
12 Sep 01	WF	4	YY01	4.711	724	4335	49
12 Sep 01	WF	4	YY02	6.566	820	6255	21
12 Sep 01	WF	4	YY07	3.892	708	3919	0
12 Sep 01	WF	4	YY09	4.902	768	4266	0
12 Sep 01	WF	4	YY11	2.099	559	1937	0
12 Sep 01	WF	4	YY12	5.086	774	4518	29
12 Sep 01	WF	4	YY14	5.123	763	4451	0
12 Sep 01	WF	4	YY22	3.901	720	3753	0
12 Sep 01	WF	5	YY23	4.962	775	4285	9
12 Sep 01	WF	4	YY25	4.432	742	4094	11
Hatchery- and Wild Origin Males: Upper Portion (Sections 1-1, 1-2, & 1-3)							
Date Introduced To Stream	Type ¹	Age	Tag No.	Weight (Kilos)	Fork Length	Estimated Un-spawned Testes Weight ³ (grams)	
12 Sep 01	HM	4	WW02	5.207	821	255.5	
12 Sep 01	HM	4	WW04	3.401	725	177.8	
12 Sep 01	HM	4	WW05	4.952	740	244.5	
12 Sep 01	HM	4	WW14	3.844	744	196.9	
12 Sep 01	HM	4	WW15	2.776	635	150.9	
12 Sep 01	HM	4	WW18	2.143	614	123.7	
12 Sep 01	HM	4	WW23	2.229	585	127.4	
12 Sep 01	HM	4	WW24	2.910	678	156.7	
12 Sep 01	HM	4	WW25	3.215	694	169.8	
12 Sep 01	HM	4	WW27	3.207	695	169.5	

Table 5. Biological traits of the hatchery- and wild-origin spring chinook placed into the observation stream in 2001 continued. . .

Hatchery- and Wild Origin Males: Upper Portion (Sections 1-1, 1-2, & 1-3)							
Date Introduced To Stream	Type ¹	Age	Tag No.	Weight (Kilos)	Fork Length	Estimated Un-spawned Testes Weight ³ (grams)	
12 Sep 01	HM	4	WW01	2.259	614	-	
12 Sep 01	Hjack	3	WW22	1.452	520	-	
12 Sep 01	WM	4	WW00	6.526	842	312.3	
12 Sep 01	WM	4	WW03	3.183	696	168.4	
12 Sep 01	WM	4	WW07	4.172	756	211.0	
12 Sep 01	WM	4	WW08	5.413	844	264.4	
12 Sep 01	WM	4	WW09	2.032	630	118.9	
12 Sep 01	WM	4	WW11	4.966	813	245.1	
12 Sep 01	WM	4	WW12	5.199	805	255.2	
12 Sep 01	WM	5	WW13	5.814	870	-	
12 Sep 01	WM	4	WW16	2.809	664	152.3	
12 Sep 01	WM	4	WW19	4.309	789	216.9	
12 Sep 01	WM	4	WW26	7.455	905	352.2	
12 Sep 01	WM	4	WW28	4.415	775	221.4	
12 Sep 01	Wjack	3	WW17	1.527	520	-	
12 Sep 01	Wjack	3	WW31	1.422	525	-	
Hatchery- and Wild Origin Females: Lower Portion (Sections 2-1, 2-2, & 2-3)							
Date Introduced To Stream	Type ¹	Age	Tag No.	Weight (Kilos)	Fork Length	Est. Fecundity ²	Eggs Lost At Tagging
19 Sep 01	HF	4	YY00	2.872	664	3827	0
19 Sep 01	HF	4	YY04	3.947	716	4057	1
19 Sep 01	HF	4	YY09	3.764	717	3983	80
19 Sep 01	HF	4	YY11	3.234	690	3519	7
19 Sep 01	HF	4	YY13	4.278	723	4451	0
19 Sep 01	HF	4	YY15	3.111	667	3344	0
19 Sep 01	HF	4	YY17	3.465	680	3825	0
19 Sep 01	HF	4	YY21	3.883	727	4068	0
19 Sep 01	HF	4	YY24	3.736	724	4030	0
19 Sep 01	HF	4	YY27	3.650	698	3946	10
19 Sep 01	WF	4	YY14	3.180	660	3136	283
19 Sep 01	WF	4	YY19	4.111	722	4507	198
19 Sep 01	WF	4	YY20	4.883	785	4534	60
19 Sep 01	WF	4	YY22	3.995	745	3983	0
19 Sep 01	WF	4	YY23	3.553	699	3319	170
19 Sep 01	WF	4	YY26	3.815	724	3780	0
19 Sep 01	WF	4	YY33	4.116	722	3857	0
19 Sep 01	WF	4	YY44	4.011	710	3740	0
19 Sep 01	WF	4	YY55	4.014	712	4127	35
19 Sep 01	WF	4	YY77	4.200	700	3727	785

Table 5. Biological traits of the hatchery- and wild-origin spring chinook placed into the observation stream in 2001 continued. . . .

Hatchery- and Wild Origin Males: Lower Portion (Sections 2-1, 2-2, & 2-3)						
Date Introduced To Stream	Type ¹	Age	Tag No.	Weight (Kilos)	Fork Length	Estimated Un-spawned Testes Weight ³ (grams)
19 Sep 01	HM	4	WW21	2.596	648	143.2
19 Sep 01	HM	4	WW27	2.703	655	147.8
19 Sep 01	HM	4	WW32	3.690	745	190.2
19 Sep 01	HM	4	WW33	4.334	756	218.0
19 Sep 01	HM	4	WW41	3.396	723	177.6
19 Sep 01	HM	4	WW44	5.246	821	257.2
19 Sep 01	HM	4	WW45	2.792	655	151.6
19 Sep 01	Hjack	3	WW34	1.109	498	-
19 Sep 01	Hjack	3	WW37	1.381	519	-
19 Sep 01	Hp male	1	No Tag	0.110	196	-
19 Sep 01	Hp male	1	No Tag	0.130	210	-
19 Sep 01	Hp male	1	No Tag	0.155	227	-
19 Sep 01	Hp male	1	No Tag	0.076	177	-
19 Sep 01	Hp male	1	No Tag	0.128	209	-
- ⁴	Hp male	1	No Tag	- ⁴	- ⁴	-
- ⁴	Hp male	1	No Tag	- ⁴	- ⁴	-
19 Sep 01	WM	4	WW04	3.987	748	203.0
19 Sep 01	WM	4	WW10	3.849	741	197.1
19 Sep 01	WM	4	WW13	4.902	801	242.4
19 Sep 01	WM	4	WW19	4.782	800	237.2
19 Sep 01	WM	4	WW20	4.008	766	203.9
19 Sep 01	WM	4	WW29	3.662	750	189.0
19 Sep 01	WM	4	WW30	3.526	714	183.2
19 Sep 01	WM	4	WW35	3.576	700	185.3
19 Sep 01	WM	4	WW50	2.321	630	131.4
19 Sep 01	WM	4	WW51	2.790	681	151.5
19 Sep 01	Wjack	3	WW49	1.776	560	-
19 Sep 01	Wp male	0	No Tag	0.009	87	-
19 Sep 01	Wp male	0	No Tag	0.006	78	-
19 Sep 01	Wp male	0	No Tag	0.008	80	-
19 Sep 01	Wp male	0	No Tag	0.009	83	-
19 Sep 01	Wp male	0	No Tag	0.005	77	-

1) Type: HF = Hatchery Female; WF = Wild Female; HM = Hatchery Male; Hjack = Hatchery Jack; Hp male = Hatchery precocious male; WM = Wild Male, Wjack = Hatchery Jack; Wp male = Wild precocious male
2) Fecundity was estimated by using multiple regression methods that used female body weight and egg weight as independent variables. An ANCOVA was performed to determine if this relationship was affected by female origin. The null hypothesis of equal slopes and y intercept could not be rejected
3) Testes weights were estimated by using the following regression formula: Predicted testes weight = 31.5 + ((0.043)(body weight in grams). This relationship was established for 4-yr-old fish and may not be valid for jacks, precocious males, and 5-yr-old individuals and therefore estimates of un-spawned testes weights on these fish were not made.
4) Two hatchery precocious males invaded the lower portion of the observation stream, thus no size information was obtained on these individuals until after their deaths.

Body Size Comparisons

One-Way ANOVAs were performed to determine if the body sizes of hatchery- and wild origin males and females placed into the upper and lower portions of the observation stream differed from one another. In the upper section the F value obtained from this test equaled 3.38 which was less than $F_{0.05(2), 3, 40}$ that equaled 3.46. Therefore the null hypothesis of equivalent body weights regardless of sex or origin could not be rejected. A similar result was obtained for the fish placed into the lower portion of the observation stream. In this case, F equaled 0.83 which again was lower than $F_{0.05(2), 3, 33}$ which equaled 3.55. The mean weights of the fish by sex, origin, and portion of the observation stream are presented in Table 6.

Table 6. The mean body weights of hatchery- and wild-origin spring chinook placed into the upper (sections 1-1, 2, 3) and lower (2-1, 2, 3) portions of the observation stream in 2001.

Upper Portion Of The Observation Stream		
Origin and Sex	Mean Body Weight In Kilograms	Range In Body Weight (Kilograms)
Hatchery Female	4.19	3.07-5.38
Hatchery Male	3.29	2.14-5.21
Wild Female	4.57	2.10-6.57
Wild Male	4.69	2.03-6.53
Lower Portion Of The Observation Stream		
Hatchery Female	3.59	2.87-4.28
Hatchery Male	3.54	2.60-5.25
Wild Female	3.99	3.18-4.88
Wild Male	3.74	2.32-4.90

Longevity Comparisons

Differences in longevity between hatchery- and wild-origin fish placed into the observation stream were assessed by using Mann-Whitney U Tests (Zar 1999). Four such tests were performed (Table 7), one for each sex for each portion of the observation stream. In the upper portion of the observation stream no differences in longevity were detected in hatchery- and wild-origin fish of the same sex. For example, the mean number of hours that hatchery-origin females lived in the upper portion of the stream equaled 67.2 h while the longevity for wild-origin females averaged 70.4 h. In addition, wild-origin males in the upper portion of the stream had an average longevity of 145.5 h and hatchery-origin males lived in this part of the stream for an average of 132.7 h. A Kruskal Wallis nonparametric One-Way ANOVA (Zar 1999) was performed to test whether any differences in longevity occurred between the four types of fish placed into the upper portion of the stream. This test also indicated that fish of the same of same sex

with hatchery and wild origins lived for the same length of time; it also showed that both types of males lived longer than females.

Similar tests were performed on the longevity data acquired from the fish placed in lower portion of the stream. In this instance, the Mann-Whitney U test that examined the longevity of females indicated that wild females (mean longevity of 90.3 h) were longer-lived than hatchery-origin females (mean longevity of 59.1 h). No difference was found in the longevity of hatchery- (mean longevity of 130.0 h) and wild- (mean longevity of 112.5 h) origin males placed into this portion of the observation stream. The Kruskal Wallis test indicated that both types of males lived longer than hatchery-origin females but no difference was found between their longevity and that of wild females.

Table 7. Results of the Mann-Whitney U Tests used to evaluate longevity differences between hatchery- and wild-origin fish of the same sex introduced into observation stream.

Upper Portion Of The Observation Stream				
Comparison	n ¹	Average Hours Alive	U Value	P ²
Hatchery (HF) vs. Wild (WF) Females	HF = 11 WF = 10	67.2 70.4	58.0	0.4144
Hatchery (HM) vs. Wild (WM) Males	HM = 11 WM = 12	132.7 145.5	70.5	0.3903
Lower Portion Of The Observation Stream				
Hatchery (HF) vs. Wild (WF) Females	HF = 10 WF = 10	59.1 90.3	79.5	0.0103*
Hatchery (HM) vs. Wild (WM) Males	HM = 7 WM = 10	130.0 112.5	42.0	0.2440
1) n equals the number of fish of each type used in the analyses 2) When p values are less than or equal to 0.05 reject the null hypothesis of no difference. P values that have an asterisk next to them indicate tests where the null hypothesis has been rejected.				

Evaluations Of Spawning Participation

Female Spawning Participation. Chi-Square analyses were used to ascertain whether hatchery and wild females had the same ability to deposit their eggs. In the upper portion of the observation stream, the combined PED (potential egg deposition) for wild females was 37,478 eggs. Conversely, the total PED for hatchery fish equaled 47, 861 eggs, and therefore the overall PED for this part of the stream equaled 85,339 eggs. Egg retention data collected showed that wild females had deposited an estimated 26,519 eggs (70.8%) while hatchery females buried an estimated 31,521 eggs (65.9%). Thus, a total of 58,040 or 68.0% of all the eggs that could have been deposited were buried in the section. The

Chi-Square that was performed on these data indicated that wild females were about 7.5% more efficient at burying their potential eggs than hatchery fish (Chi-Square with Yates correction equaled 74.1 >> Chi-Square $(0.05)_2$ 1 df = 3.841). An identical analysis was performed on the hatchery and wild females spawning in the lower section of the observation stream. In this case wild females buried an estimated 91.5% of their eggs. Hatchery females, on the other hand, deposited 75.6.5% of theirs. A combined total of 64,917 eggs, 35,414 from wild females and 29,503 from hatchery fish were placed into this portion of the stream. The Chi-Square test once again showed that wild females were 21.1% more capable of burying their eggs than contemporary hatchery fish (Chi-Square equaled 595.9 >> Chi-Square $(0.05)_2$ 1 df = 3.841).

A series of linear regression analyses were performed to evaluate whether body weight affected the percentage of eggs females deposited. Four such analyses were performed, one for each type of female placed into the two portions of the observation stream. The independent variable in these analyses was body weight at the time of entrance into the observation stream while the dependent variable was the arcsine transformed (Zar 1999) percent spawned value estimated for each female. None of these tests were significant (Table 8) in addition, the slopes in the data sets were both positive and negative, suggesting that female size and the ability to deposit eggs were not positively or negatively related to one another in the observation stream.

Table 8. Results of linear regression analyses performed to assess the relationship between body weight in adult hatchery- and wild-origin females and their ability to deposit eggs in the observation stream.

Upper Portion Of The Observation Stream				
Regression	n	Slope ¹	F	P Value ²
Hatchery Female Body Weight vs. Percent Spawned (Arcsine Transformed)	11	-20.96	1.85	0.2068
Wild Female Body Weight vs. Percent Spawned (Arcsine Transformed)	9	-6.84	1.04	0.3415
Lower Portion Of The Observation Stream				
Hatchery Female Body Weight vs. Percent Spawned (Arcsine Transformed)	10	+15.30	0.48	0.5086
Wild Female Body Weight vs. Percent Spawned (Arcsine Transformed)	10	+12.49	0.76	0.4102
1) Slope equals the arcsine transformed percent spawned value that changes per kilogram of female weight. Therefore a negative slope indicates that a negative relationship exists between female weight and percent spawned values while a positive slope suggests the opposite.				
2) A p value less than or equal to 0.05 would indicate a significant relationship				

The relationship between percent spawned and longevity in hatchery- (diamonds) and wild-origin females (squares) that spawned in the lower section of the observation stream is shown in Fig 1. It appears from this scatter diagram that females need to be alive for set number of hours before they can deposit all of their eggs. Sokal and Rholf (1995) suggest that such data can be examined by using isotonic regression. With this method it was possible to test whether a consistent increase in spawning success was a function of ranked hours alive. Four such regressions were performed, one for each type of female

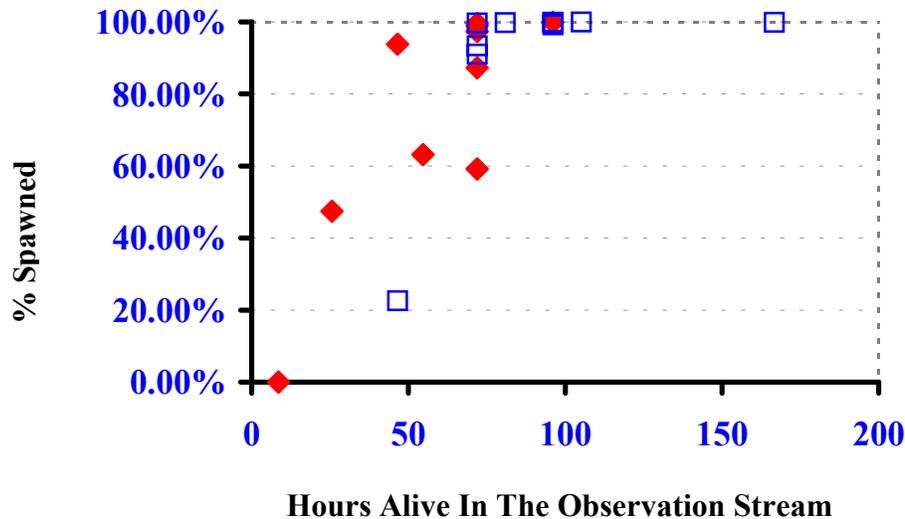


Fig. 1. The relationship between hatchery- and wild-origin female longevity and percent spawned values in the lower portion of the observation stream. Diamonds depict data collected on hatchery fish while squares indicate information obtained on wild females.

placed into the upper and lower portions of the observation stream. All were significant; the percentage of eggs hatchery- and wild-origin females deposited increased during their early residency and reached an asymptote after they had resided in the stream for a minimum of 48 to 96 h (Table 9). In the upper portion of the stream wild females that lived for 48 h or more had an average percent spawned value of 98.6%. Hatchery females, on the other hand, had to live for 71 hrs to achieve a comparable average percent spawned value of 94.6%. A similar trend was observed in the lower portion of the observation stream. Here the spawning success of wild females rose steeply as longevity increased over the first 72 hrs and fish that lived longer than that were often able to deposit all of their eggs (Fig. 1). The capacity of hatchery females to deposit eggs in this portion of the observation stream never reached a plateau. Instead it increased continuously, culminating with the hatchery female that lived for 96 h who had deposited 99.9% of her eggs.

Table 9. Results of the isotonic regressions that evaluated the relationship between hatchery- and wild-origin female longevity and their percent spawned values.

Upper Portion Of The Observation Stream			
Isotonic Regression	n	E ² Value ¹	P Value ²
Hatchery Females: Ranked Longevity (h alive in the observation stream) vs. Arcsine of Percent Spawned Value	11	0.8388	0.0020**
Wild Females: Ranked Longevity (h alive in the observation stream) vs. Arcsine of Percent Spawned Value	9	0.71633	0.0260*
Lower Portion Of The Observation Stream			
Hatchery Females: Ranked Longevity (h alive in the observation stream) vs. Arcsine of Percent Spawned Value	10	0.83049	0.0040**
Wild Females: Ranked Longevity (h alive in the observation stream) vs. Arcsine of Percent Spawned Value	10	0.96281	0.0020**
1) The E ² statistic is calculated by dividing the sums of squares groups by the total sums of squares (Sokal and Rholf 1995). 2) A single asterisk indicates the test was significant at an alpha of 0.05 and a double asterisk indicates it was significant at an alpha of 0.01.			

Male Spawning Participation. Both of our estimates of male spawning participation, PGD (percent gonad depletion) and PRT (testes weight at death/male weight at maturity) assume that hatchery- and wild-origin males have similar gonadal-somatic index values (Testes Weight/Body Weight at maturity). Fleming and Gross (1992) however, found that hatchery coho had larger testes than wild counterparts. Consequently, we performed an ANCOVA to test whether hatchery- and wild-spring chinook returning to the Upper Yakima had similar body weight x testes weight relationships. The null hypothesis of equal slopes (increase in testes weight per increment of body weight) could not be rejected ($p = .7331$). Moreover, the test also failed to reject the null hypothesis of equivalent y-intercepts ($p = .0770$). However, the sample sizes used in the regressions (hatchery males $n = 7$; wild males $n = 16$) were small. When more of this type of information becomes available additional tests will be performed to evaluate this assumption. It is important to do so, because if hatchery males for example, have higher gonadal-somatic index values than wild individuals their PGD and PRT values would be underestimates of their spawning participation.

Mann-Whitney U tests were used to compare the PGD and PRT values obtained on hatchery- and wild-males. The results of these tests (Table 10) showed that hatchery and wild-males had similar spawning participation values in both the lower and upper portion of the stream. We also performed linear regressions on male body size (the independent

variable) and arcsine transformed PRT values (the dependent variable) to see if body weight affected estimated spawning participation. The results indicated that the largest males generally had lower PRT values than smaller competitors (Table 11). The affect varied by type of male and location. For example, body size explained 27% of the variation in PRT in wild males in the upper section but a non-significant relationship was found between male weight and PRT values in the hatchery fish placed into this portion of the stream. When data from all the males was combined, male weight explained 17% of the variation associated with PRT values. Conversely, in the lower section, larger hatchery males had lower PRT values (adjusted $r^2 = .56$) whereas this relationship was not significant in the wild fish. The regression that used data from both hatchery- and wild-males placed into the lower section had an adjusted r^2 of .15 but a p value of .07. Similar linear regressions were performed between male body weights and PGD values. However, in this instance, none of the relationships were significant indicating that male weight had a minimal effect on PGD values (Table 11). Yet, in every analysis, except

Table 10. Results of the Mann-Whitney U Tests performed to evaluate differences in spawning participation of hatchery and wild males as estimated by PRT (testes weight at death/body weight at maturity) and PGD (testes wt at death/predicted weight of testes at maturity) values.

Upper Portion Of The Observation Stream				
Comparison	n ¹	Average Values ²	U Value	P Value ³
Hatchery (HM) vs. Wild (WM) Male PRT Values	HM = 11 WM = 12	4.1% 3.8%	70.0	0.4028
Hatchery (HM) vs. Wild (WM) Male PGD Values	HM = 11 WM = 12	83.5% 80.5%	68	0.4508
Lower Portion Of The Observation Stream				
Hatchery (HM) vs. Wild (WM) Male PRT Values	HM = 7 WM = 10	3.6% 4.2%	41	.2791
Hatchery (HM) vs. Wild (WM) Male PGD Values	HM = 7 WM = 10	72.4% 82.3%	43	.2175
1) n equals the number of hatchery and wild males of each type compared in the Mann Whitney U tests 2) PRT equals testes wt at death divided by body weight at maturity. Therefore low PRT values should be associated with higher spawning participation. PGD values are calculated by dividing testes weight at death by the testes weight predicted for a male based on his body weight at maturity. Low PGD values also indicate higher spawning participation in males. For example, on average the hatchery males in the lower portion of the observation stream expended approximately 28% of their predicted testes weights during their reproductive lifetimes. 3) A p value less than or equal to 0.05 would indicate a significant difference.				

Table 11. Results of the linear regressions that evaluated the relationships between body size and PRT and PGD values obtained from hatchery and wild males spawning in the observation stream.

Upper Portion Of The Observation Stream				
Regression	n	Slope	F	P Value
Hatchery Male Body Weight (Kilograms) vs. PRT (Arcsine Transformed)	11	-0.54	0.7147	0.4198
Wild Male Body Weight (Kilograms) vs. PRT (Arcsine Transformed)	12	-0.90	5.2611	0.0447*
Hatchery and Wild Male Body Weight (Kilograms) vs. PRT (Arcsine Transformed)	23	-0.68	5.6498	0.0270*
Hatchery Male Body Weight (Kilograms) vs. PGD (Arcsine Transformed)	11	-4.37	0.5053	0.4952
Wild Male Body Weight (Kilograms) vs. PGD (Arcsine Transformed)	12	-5.64	2.7699	0.1270
Hatchery and Wild Male Body Weight (Kilograms) vs. PGD (Arcsine Transformed)	23	-4.41	2.9132	0.1026
Lower Portion Of The Observation Stream				
Hatchery Male Body Weight (Kilograms) vs. PRT (Arcsine Transformed)	7	-1.89	8.6388	0.0323*
Wild Male Body Weight (Kilograms) vs. PRT (Arcsine Transformed)	10	-0.29	0.1616	0.6982
Hatchery and Wild Male Body Weight (Kilograms) vs. PRT (Arcsine Transformed)	17	-1.03	3.8037	0.0700
Hatchery Male Body Weight (Kilograms) vs. PGD (Arcsine Transformed)	7	-11.19	4.6974	0.0824
Wild Male Body Weight (Kilograms) vs. PGD (Arcsine Transformed)	10	+3.02	0.2119	0.6575
Hatchery and Wild Male Body Weight (Kilograms) vs. PGD (Arcsine Transformed)	17	-3.62	0.6471	0.4337

one the slopes of the regression lines were negative. This indicates that there was a consistent trend for larger males to possess smaller PRT and PGD values.

Reproductive Success Comparisons

A pedigree analysis was performed on 970 randomly chosen fry collected from the upper portion of the observation stream. Altogether 18,960 fry were captured from this section and therefore about 5% of the offspring originating from the adults placed into this section were examined to determine which adults had produced them. In the lower section, a total of 714 fry were used in a pedigree analysis. Here a total of 42,263 fry were collected so approximately 1.7% of the progeny produced by the adults were employed to estimate the reproductive success each adult.

The pedigree assignments showed that the reproductive success of males was more variable than that experienced by females. In the upper section for instance, the coefficient of variation associated with fry production was 171% in males and 88% in females (Fig. 2). Most of the females placed into this part of the stream produced some offspring while over half the males in the same section produced very few or no offspring.

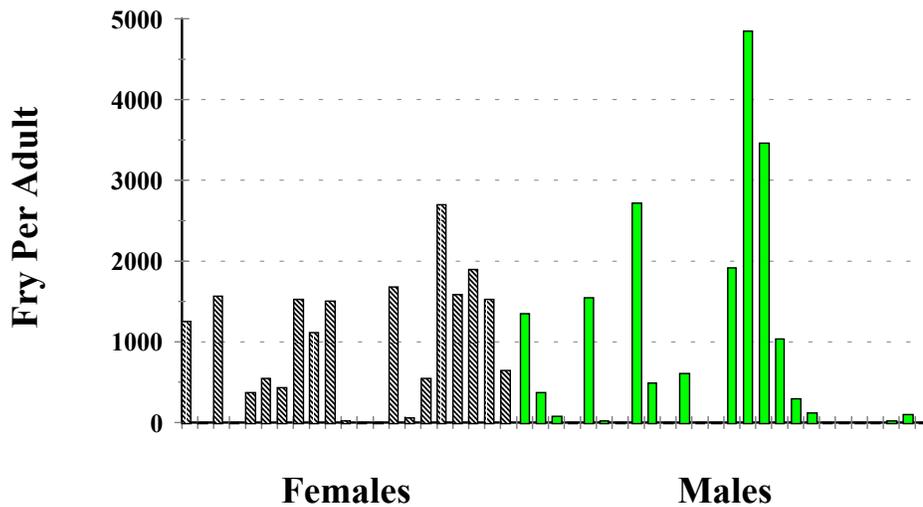


Fig. 2. Fry production from the females (striped bars) and males (solid bars) placed into the upper portion of the observation stream in 2001.

Female Reproductive Success. Two different Chi-Square tests were used to compare the reproductive success of hatchery and wild females. The first examined their ability to convert eggs into fry. This test evaluated the capacity to deposit eggs and their survival to the fry stage. The second test compared the ability of eggs spawned by the two types of females to create fry. It represents an attempt to see if redd quality varied because of female origin. In the upper section, wild females converted 28%, and hatchery females 17%, of their eggs into fry. Thus wild females were 63% better than hatchery fish at

producing progeny from their eggs (Chi-Square = 57.1 >> Chi-Square_{(0.05)2 1 df = 3.841}) (Fig. 3). Part of this difference was caused because hatchery females were not as capable of burying their eggs as wild fish (*see* page 17). Furthermore, the survival of eggs

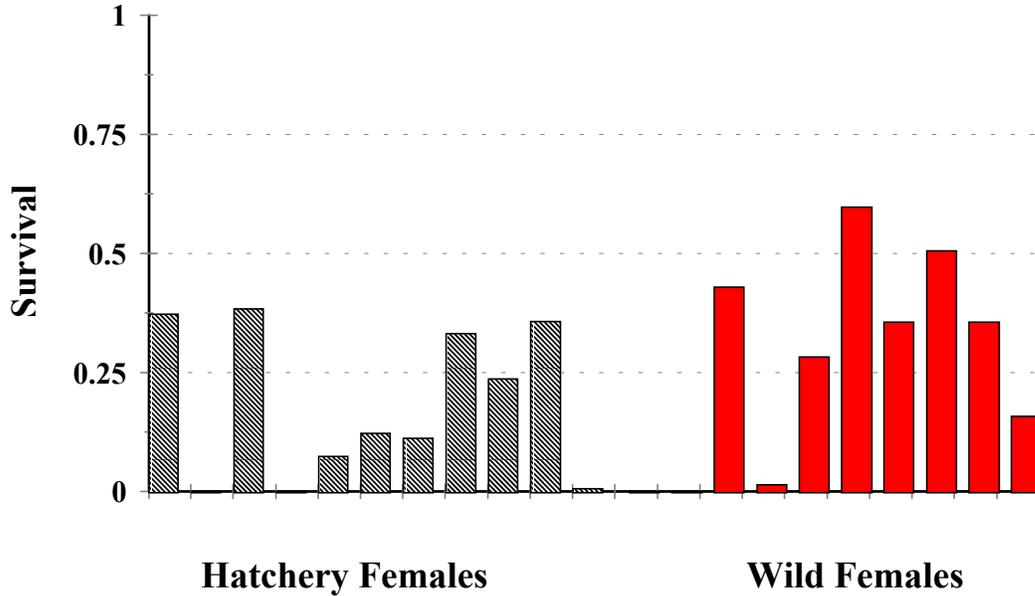


Fig. 3. The production of fry from the eggs brought into the upper portion of the observation stream by hatchery and wild females.

deposited by hatchery and wild origin females clearly differed (Fig. 4). Approximately

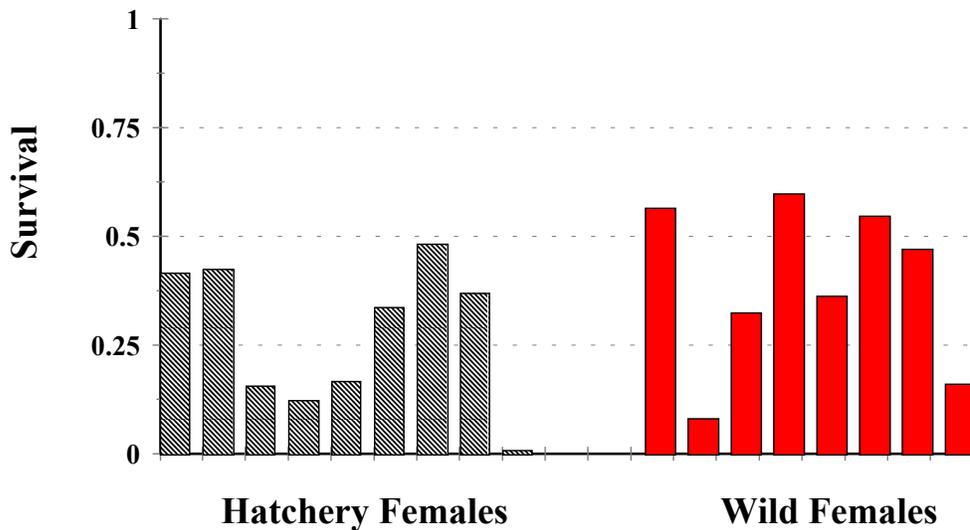


Fig. 4. The survival of eggs deposited by hatchery- and wild-origin spring chinook females spawning in the upper portion of the observation stream.

26% of the eggs deposited by hatchery females produced fry while 40% of those originating from wild females survived (Fig. 4). Consequently, wild females were 52% better at producing fry from buried eggs than hatchery females (Chi-Square = 41.8 >> Chi Square $(_{0.05})_2$ 1 df = 3.841). Comparable results occurred in the lower section. Here wild females were 51% more effective at producing fry from their eggs than hatchery fish (Chi-Square = 30.3 >> Chi Square $(_{0.05})_2$ 1 df = 3.841) and 25% better at creating fry from the eggs they deposited in the observation stream (Chi-Square = 8.4 > Chi Square $(_{0.05})_2$ 1 df = 3.841).

Male Reproductive Success. Chi-Square analysis was also used to determine if any differences existed in the ability of hatchery and wild males to produce offspring. In the upper section hatchery and wild males were represented by two different life history types, jacks (3-yr-old males) and those that matured at ages four and five (Table 5). The Chi-Square test indicated that the ability to produce offspring was not equivalent (Chi-Square = 129.9 >> Chi-Square $(_{0.05})_2$ 3 df = 7.815). Wild jacks fathered the fewest fry (0.25% per jack). The analysis was performed again without including the paternity data from these fish. This test produced another significant Chi-Square value (55.3 >> Chi-Square $(_{0.05})_2$ 2 df = 5.991) and disclosed that wild males fathered a greater number of fry than expected (5.14% per male). A final Chi-Square test evaluated whether hatchery jacks and hatchery males differed in their capacity to father males. In this instance the null hypothesis could not be rejected (Chi-Square = 0.0002 << Chi Square $(_{0.05})_2$ 1 df = 3.841). Each hatchery male fathered 3.1% of the fry produced from the section while the single hatchery jack produced 3.2% of the fry (Fig. 5). On average, wild males were 61% more effective at producing offspring than the hatchery males and jacks.

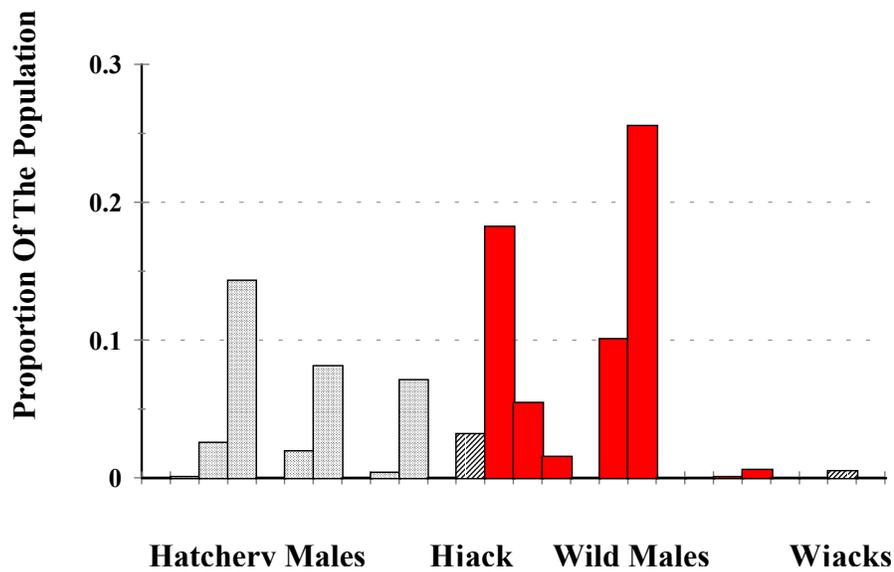


Fig. 5. The proportion of fry produced by hatchery and wild males spawning in the upper portion of the observation stream. Each bar represents a single male. Hatchery males are represented by stippled bars, the hatchery jack by a striped bar, wild males by solid bars, and wild jacks by striped bars.

Hatchery and wild males expressing three different life history strategies, precocious males that matured at ages 0+ and 1+, jacks that matured as 3-yr-old fish and four-year-old males, were introduced into the lower portion of the observation stream. A similar series of Chi-Square tests were performed to ascertain whether differences existed in their capacities to produce offspring (Fig. 6). These tests revealed that wild precocious (Wp

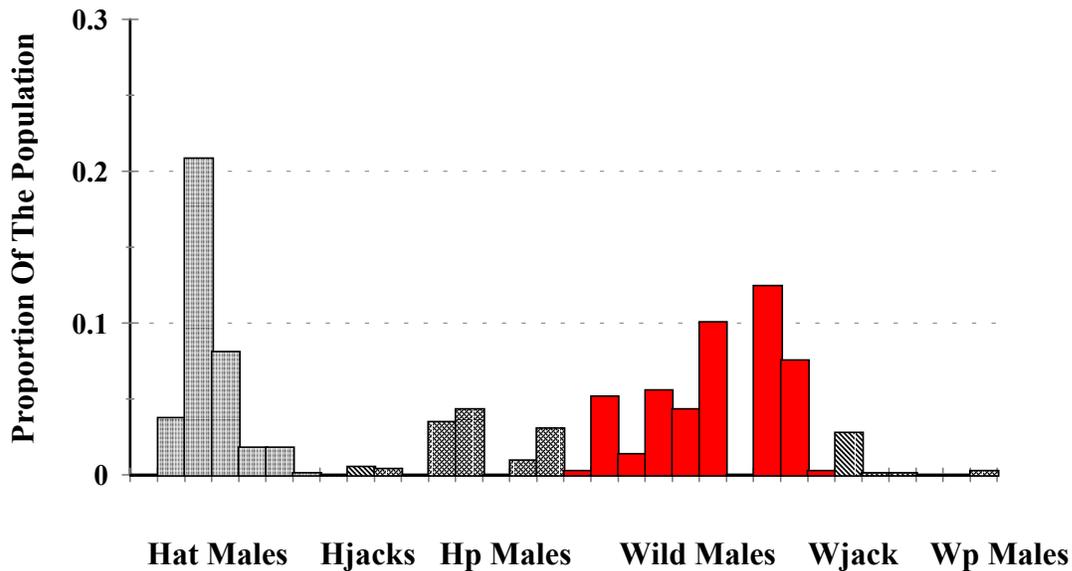


Fig. 6. The proportion of fry produced by hatchery and wild males spawning in the lower portion of the observation stream in 2001. Each bar represents a male. From left to right, hatchery males are symbolized by stippled bars, hatchery jacks by striped bars, hatchery precocious males by crosshatched bars, wild males by solid bars, wild jacks by striped bars, and wild precocious males by crosshatched bars.

males) fathered the fewest fry of any of the different male types examined (Chi-Square = 299.2 >>11.07 (0.05)₂ 5 df). Hatchery jacks were slightly more productive than the Wp males but less successful than the hatchery precocious males and the wild jacks (Chi-square = 23.2 >>5.991 (0.05)₂ 2 df) who had comparable reproductive success (Chi-Square = 1.2 < 3.841 (0.05)₂ 1 df). In addition, no difference was found in the reproductive success of the 4-yr-old hatchery and wild males (Chi-Square = 1.4 < 3.841 (0.05)₂ 1 df) who fathered the most fry of any of the male life-histories present in this part of the observation stream.

Chi-Square tests were also performed to see if wild and hatchery males fertilized a disproportionate number of eggs originating from either wild or hatchery females. To perform these tests we had to estimate the number of eggs each type of male fertilized by taking into account that hatchery and wild females had different egg-to-fry survival rates. In the upper portion of the stream, for example, eggs deposited by wild females survived 1.51 times greater than those laid by hatchery females. In this section, wild males fathered a total of 598 fry out of the 970 that underwent the pedigree analysis. Two hundred and sixty-three of them originated from hatchery females and three hundred and thirty-five came from wild females. To perform a Chi-Square test to see if mating

occurred in a random fashion, the observed number of fry produced from hatchery females was adjusted by multiplying it by 1.51. This new value equaled the number of fry that hatchery females would have produced if their egg-to-fry survival rates had been equal to that experienced by the wild females. The null hypothesis being tested is that males will fertilize eggs originating from wild and hatchery females in proportion to their abundance. Since hatchery females deposited 54% of the eggs in this part of the experimental stream, the adjusted value was multiplied by this percent to obtain an expected value. The Chi-Square performed to test whether wild males produced more or less offspring than expected from hatchery and wild females is shown below to serve as an example of the calculations described above (Table 12).

Table 12. The Chi-Square test used to evaluate whether wild males fertilized eggs from hatchery and wild females in a non-random fashion.

Origin Of Female Parent	Observed Number Of Fry ¹	Adjusted Number of Fry ²	Expected Number of Fry ³	Chi-Square Value Using Yates Correction Factor
Hatchery	263	399.2	398.7	.0000037
Wild	335	335	335.5	.0000044
Sums	598	734.2	734.2	.0000081

- 1) This is the number of fry identified in the pedigree analysis that were fathered by wild males. In this part of the stream, wild males produced 263 hatchery female x wild male fry and 335 wild female by wild male fry
- 2) Since eggs spawned by wild females survived 1.51 times greater than those deposited by hatchery females the number of fry produced by hatchery females was multiplied by 1.51 to produce an estimate of the number of hatchery eggs actually fertilized by wild males.
- 3) Expected values were obtained by multiplying the adjusted number of fry times the proportion of eggs originating from each type of female. In this instance 54% of all the eggs deposited came from hatchery females. Therefore the expected number of such fry equals 0.54 times 734.2 or 399.2 fry. Similarly the expected number of wild-by-wild fry equaled 734.2 times 0.46 the proportion of eggs deposited that had originated from wild females or 335.5 fry.

The null hypothesis of this Chi-Square could not be rejected ($.000008 \ll 3.841_{(0.05)2} 1$ df). Chi-Square values of 3.144 for hatchery males in the upper section, 0.92 for wild males, and 2.75 for hatchery males in the lower section were obtained on the remaining tests. None of these values were significant and therefore males appear to fertilize eggs produced from wild and hatchery females in proportion to their abundance.

Figures 2, 5, and 6 illustrate that a great deal of variation exists in the reproductive success of both hatchery and wild males. Previous researchers have suggested that relative size can be an important factor in determining the reproductive success of males competing among themselves for females. Generally, larger males are expected to dominate smaller opponents and thus obtain more opportunities to fertilize eggs. Linear regression analyses were performed to ascertain whether male reproductive success in the observation stream was dependent upon male size. Six such analyses were performed.

The independent variable was male weight in kilograms while the dependent variable was the arcsine-transformed (Zar 1999) percentage of fry fathered by each male placed into either the upper or lower portion of the stream. Percentage values were obtained by dividing the number of fry assigned to a male in its pedigree analysis by the total number of fry analyzed. Therefore a male that fathered 20 fry out of the 970 analyzed in the upper section was assumed to have fathered 2.062% of the fry produced from this section. The results of these analyses are shown in Table 13. In every analysis there was a positive

Table 13. Results of the linear regressions that evaluated the relationships between body size and reproductive success (RS) values in hatchery and wild males spawning in the observation stream.

Upper Portion Of The Observation Stream					
Regression	n	Slope	Adjusted r square ¹	F	P Value ²
Hatchery Male Body Weight vs. Male RS (Arcsine Transformed)	11	+0.46	-0.1068	0.0039	0.8558
Wild Male Body Weight vs. Male RS (Arcsine Transformed)	12	+4.58	0.4030	8.4263	0.1576*
Hatchery and Wild Male Body Weight vs. Male RS (Arcsine Transformed)	23	+2.85	0.1810	5.8629	0.0246*
Lower Portion Of The Observation Stream					
Hatchery Male Body Weight vs. Male RS (Arcsine Transformed)	7	+7.93	0.7031	15.2072	0.0114*
Wild Male Body Weight vs. Male RS (Arcsine Transformed)	10	+2.88	-0.0005	0.9950	0.3477
Hatchery and Wild Male Body Weight vs. Male RS (Arcsine Transformed)	17	+5.38	0.3278	8.8016	.0096**
1) Also referred to as the coefficient of determination it indicates the proportion of variation in the dependent variable (male RS) explained by the independent variable (Male body weight) 2) A single asterisk indicates significance at the alpha 0.05 level, while two asterisks indicate significance at the 0.01 level or greater.					

slope and in four of them significant relationships occurred with male body size explaining anywhere from 18 to 70% of the variation in male reproductive success. In two instances (hatchery males in the upper portion and wild males in the lower part of the

observation stream), male body size apparently had no influence on reproductive success. Nonetheless, when data from both hatchery and wild males were combined, male size explained 18 (upper) to 33% (lower) of the variation associated with their reproductive success.

Clearly several factors besides relative size may affect male success. An obvious one would be the behavior exhibited by an individual while it is on the spawning grounds. In our previous report (Schroder et al. 2003) we described how behavioral observations were made on the fish placed into the observation stream. Briefly two types of observations were made, scan and focused. Scan observations lasted for three to five minutes. During that time the location, color pattern, reproductive status, and frequency of agonistic and courting behavior of an individual fish was recorded onto audiotape. Focused observations were directed toward females that were preparing nests and the courtship and agonistic behavior they and the males and females they interacted with expressed. The goal of each focused observation was to obtain about 120 minutes of pre-spawning behavior and up to 60 minutes of post spawning activities. Like the scan observations the activities of the observed fish were recorded on audiotape. Transcriptions of the tapes made on hatchery and wild fish spawning in the observation stream in 2001 are still being made. However, behavioral observations made on wild fish placed into the stream in 2000 have been analyzed and some of the findings from these tapes will be presented along with some data collected in 2001 to provide insights on the behavioral features that appear to be directly linked to male reproductive success. Most of this information was gathered on the fish placed into section 1-1 in 2000. Eight 4-yr-old males, 2 jacks and eight females were placed into this part of the stream (*see* Schroder et al. 2003 for additional details about these fish. Fig. 7 illustrates the variation in male reproductive success that occurred in this section. It is comparable to what was

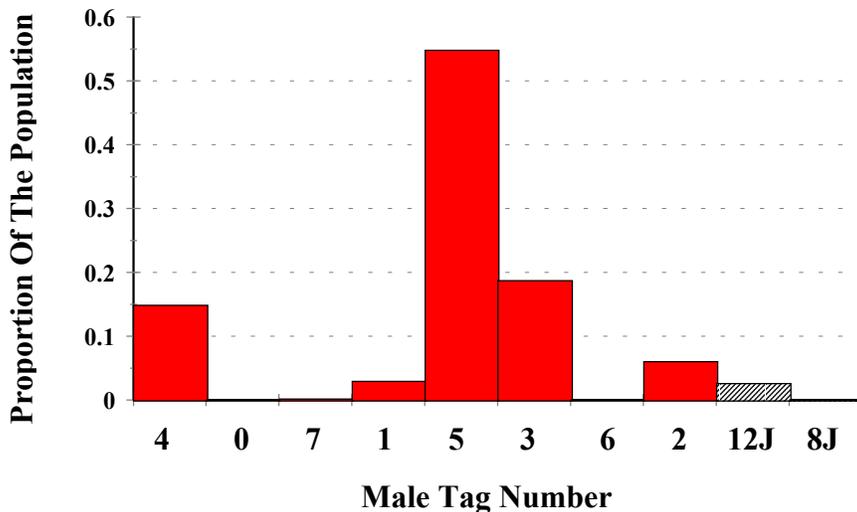


Fig. 7. The proportion of offspring fathered by the males placed into section 1-1 in 2000. Each bar represents a single male. Solid bars symbolize 4-yr-old males while jacks (J) have bars with stripes.

found in the observation stream in 2001 as the coefficient of variation associated with male reproductive success equaled 170.7%. Two masculine features should be associated with their reproductive success, their relative dominance over competing males and how females respond to them. We developed two measures of male dominance. The first one evaluated overall dominance by using scan data to determine the number of times a male attacked other fish and how often he was attacked. These data were used to create dominance index by dividing the number of times a male attacked other fish by the total number of agonistic interactions that were recorded for that individual. The sex of the fish a male attacked or was attacked by was noted and so it was also possible to calculate how often males were attacked by females. An ordinal rank of male dominance was also produced. In this case how often males attacked or were attacked by individual males was used. If for example, a male attacked a male more often than he was attacked by that fish he was given a score of 1. If a particular male dominated him or he was never observed to interact with that male a score of 0 was given. The ordinal rank of a male was ascertained by summing the scores he achieved with each male in his section. The data used to create an overall dominance value and ordinal rank value for a male (Male # 3) placed into section 1-1, 2000 is shown below to illustrate how these calculations were made. Besides these interactions with males, Male 3 was also attacked two times by females, consequently 216 interactions

Table 14. The data used to calculate an overall dominance and ordinal ranking score for Male # 3, a fish placed into section 1-1 in 2000.

Calculating Dominance Scores For Male # 3: Section 1-1, 2000			
Male Tag No.	No. Of Times Opponent Attacked Male # 3	No. Of Times Male # 3 Attacked Opponent	Ordinal Score
0	0	25	1
1	0	11	1
2	1	22	1
4	0	26	1
5	26	4	0
6	1	10	1
7	0	26	1
8	0	0	0
12	0	15	1
Unk ¹	2	45	
TOTALS	30	184	7
1) The tag numbers of the individuals that interacted with the fish being observed were not always identified because of surface water disruptions, reflection and other causes. When that occurred its behavior and sex were recorded and it was referred to as an unknown male or female.			

were recorded that involved this fish. His overall dominance score equaled 184/216 or 85.19% and his ordinal rank was 7. A total of 41 scan observations were made on Male #

3 and during two of them he was attacked by a female so he was provided with a 4.88% score (2/41) for the percentage of observations that he received attacks from females. In addition, on 26 out of the 41 scans Male # 3 was seen courting or next to a female. Consequently, he was given a 63.4 % courting score. Every male placed into section 1-1 had similar values calculated on them based on the observations that were made while they courted and spawned with females.

During the course of making these observations we discovered that the fish exhibited a variety of color patterns that ranged from almost entirely black to fish with light green backs, dark purple-blue sides and gray to white ventral surfaces (Fig. 8). We loosely placed these patterns into three categories referred to as “dark”, “medium”, and “stripe”. The reproductive condition and social status of the fish possessing these patterns were

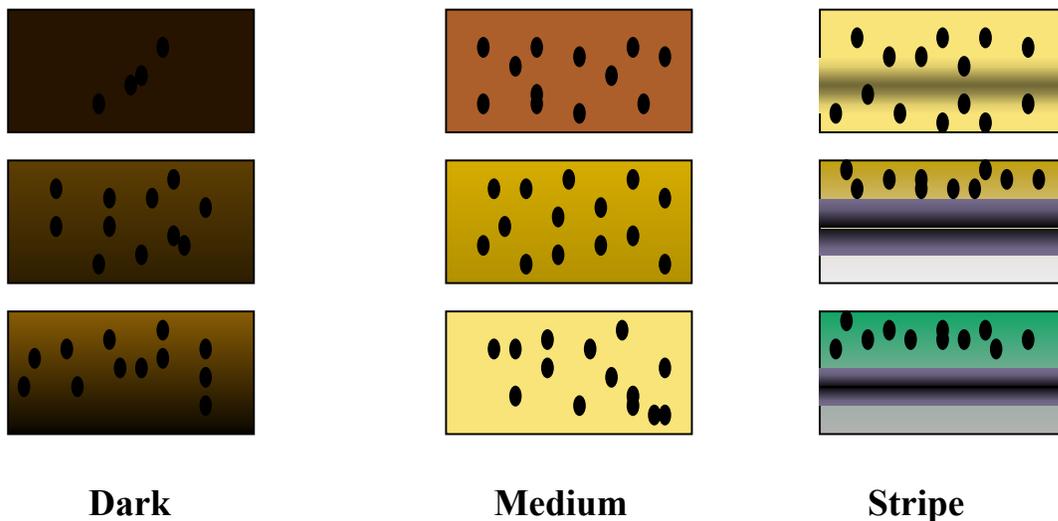


Fig. 8. Schematic representations of the different nuptial color patterns found on spring chinook spawning in the observation stream.

noted to determine if links between nuptial coloration and behavior could be made. The background coloration in the examples shown in Fig. 8 are generally brown and yellow, however, depending upon light conditions these could shift toward a steely-gray blue color. Regardless of the background coloration, a consistent gradation between a uniformly dark to a pronounced stripe pattern occurred. Thus, the nine blocks shown above represent just a few of the many variations that exist between these two extreme patterns. Table 15 shows that females that had established territories and were actively digging nests or defending their redd sites often had pronounced stripes. Fish that were still searching for a territory usually possessed the dark or medium patterns. Once they began some exploratory digging these patterns started to disappear and a faint or more fully developed stripe would occur. Color patterns were also strongly linked to masculine behavior (Table 16). Dominate males courting females were usually dark while non-courting sub-dominant males typically had the stripe pattern. Female agonistic behavior toward males was influenced by their color patterns (Table 17); males

possessing stripes were more likely to be attacked than those having the dark or medium patterns. These results indicate that a considerable amount of information on the reproductive status of females and social status of males can be obtained by monitoring their color patterns.

Table 15. The presence of the dark, medium, and stripe color patterns on wild female spring chinook reproducing in the observation stream in 2000.

Observed Color Pattern	Reproductive Status Of Observed Female			
	Nomad ¹	Exploratory Digging ²	Territorial ³	Early Spent ⁴
Dark	51%	14%	11%	0%
Medium	39%	36%	4%	0%
Stripe	10%	50%	86%	100%

Ninety-six observations on adult females placed into the observation were used to produce this table

- 1) Nomadic females are fish that are wandering throughout the observation stream and have exhibited no apparent digging or territorial behavior.
- 2) Prior to establishing a territory or location where they can bury their eggs females often will dig in widely separated locations this behavior is referred to as exploratory digging.
- 3) Territorial females active defend a portion of the streambed and dig nests and create a redd in this location
- 4) A female that is completely finished with her spawning activities is referred to as "spent". So far the only color pattern observations we have on spent females have occurred soon after they were finished spawning. Whether there color patterns may change as they continue to age is unknown at this time.

Table 16. The presence of the dark, medium, and stripe color patterns on male spring chinook spawning in the observation stream in 2000.

Observed Color Pattern	Behavioral Status Of Observed Male			
	Sub-Dominate & Solitary ¹	Sub-Dominate With Female ²	Dominate & Solitary ³	Dominate With Female ⁴
Stripe	82%	0%	2%	4%
Dark	5%	9%	5%	81%

One hundred and one observations were used to create this table. Information on the color patterns found on satellite males was not included in this table.

- 1) Sub-dominant solitary males are those individuals that are alone and are attacked more often than they attack their opponents
- 2) Sub-dominant males with females are individuals that are courting females but who are attacked more times they attack their opponents
- 3) Dominate and solitary males are fish that are not courting females who attack opponents more often than they are attacked
- 4) Dominate with female are males that are actively courting females who attack their opponents more often than they are attacked.

Table 17. The incidence of female attacks on males possessing the dark, medium, or stripe color pattern in section 1-1, 2000.

Color Pattern Of Male	Percentage Of The Time Attacked By Females
Dark	15%
Medium	10%
Stripe	75%

A summary of the behavioral traits and body sizes of the wild males placed into section 1-1 in 2000 is presented in Table 18. The relationship between these traits and the reproductive success of each male is shown in Table 19. As expected males with high

Table 18. Behavioral and morphological traits possessed by the wild males spawning in section 1-1 in 2000.

Male #	Body Wt Kilograms	Overall Dominance	Ordinal Rank	% Of Obs. Females Attacked Male	% Of Time In Dark Color	% Of Obs. That Male Court Females
0	3.590	18.63%	2	39.29%	18.18%	25.00%
1	2.902	7.14%	1	42.86%	0.00%	4.76%
2	3.108	37.33%	4	19.05%	0.00%	38.10%
3	4.603	85.19%	8	4.88%	100.00%	63.41%
4	3.716	39.13%	7	25.00%	77.78%	62.50%
5	5.092	92.37%	9	0.00%	100.00%	66.67%
6	2.057	8.93%	2	43.75%	0.00%	12.50%
7	4.126	53.21%	5	28.00%	18.18%	36.00%
8 jack	0.849	NO ¹	1	NO	NO	NO
12 jack	1.125	9.46%	2	45.83%	0.00%	4.17%

A total of 915 observations were used to characterize the behavioral traits presented in this table

- 1) Jack 8 was only observed several times and therefore not enough information was gathered on this fish to provide an estimates for overall dominance, frequency of female attack, time observed in the dark pattern or on the percentage of observations the male was observed next to or courting a female.

overall dominance and ordinal dominance ranks were more successful than competitors that had lower scores in these traits. The percentage of time males spent courting females and the amount of time they had dark color patterns were also positively related to reproductive success. Moreover a positive but non-significant relationship between body weight and reproductive success occurred in this population. Somewhat surprisingly,

there was a strong negative relationship between frequency of female attacks and male reproductive success. An obvious analytical step that we have not yet performed is to use step-wise multiple regressions to evaluate the relative importance of male origin, body size, and the other traits shown in Tables 18 and 19 on male reproductive success. It is highly likely that many of these traits are strongly correlated with one another and therefore some will have to be combined or dropped before such analyses can be performed in order to avoid the effects of multicollinearity (Zar 1999).

Table 19. The affect of body size and behavior on the reproductive success (RS) of the males placed into section 1-1 in 2000.

Relationship	Result	Statistical Result	P Value
Body Weight vs. Reproductive Success	Heavier males had greater RS	Adjusted R ² = .358*	0.0398
Overall Dominance vs. Reproductive Success	Males with high dominance had greater RS	Adjusted R ² = .578*	0.0106
Ordinal Rank vs. Reproductive Success	Males that had high ordinal rank scores had greater RS	Tau = .650**	0.0044
% Of Observations With Female Attacks vs. Reproductive Success	Males that were most often attacked by females had low RS	Adjusted R ² = .743**	0.0017
% Of Time Dark vs. Reproductive Success	The length of time spent in the dark pattern was positively linked to RS	Adjusted R ² = .420*	0.0351
% Of Observations Males Courted Females vs. Reproductive Success	Males that commonly courted females had higher RS values than rivals who courted less	Adjusted R ² = .685**	0.0036

DISCUSSION

The data presented above represent one of the first attempts to compare the reproductive success of naturally spawning wild- and hatchery-origin spring chinook. All the hatchery fish used in these comparisons were derived from wild parents who were native to the Upper Yakima River that had been artificially spawned. The differences we observed occurred after a single generation of exposure to hatchery conditions. Therefore it is likely that most of the divergences expressed owe their origins to the early environmental conditions the fish experienced. Similar evaluations occurred in 2002 and additional ones will be conducted in future years. We believe it will be important to compare the findings reported above with results generated from the studies that were carried out in 2002, and that will take place later on. Such an approach will allow us to see if consistent differences in the performance of these fish occur over multiple years. If they do then it will be clear that exposure to hatchery conditions, even for a single generation can precipitate significant biological effects in both sexes.

In some instances results were mixed. For example, in the upper portion of the stream we found that no difference in the longevity of hatchery-origin and wild females occurred while in the lower section wild females did live for a longer period of time. As the isotonic regressions illustrated, longevity in females can be linked to reproductive success. The fish have to live for a minimum number of hours to deposit all of their eggs and create a successful incubation environment for their offspring. We did, however, find consistent differences between hatchery and wild females in their ability to deposit eggs and in the survival of their deposited eggs. Wild females were better at depositing eggs and their eggs achieved higher survival rates.

Male origin did not affect longevity nor did it affect the measures we used to estimate spawning participation, percent gonad depletion (PGD) and percent retained testes (PRT). Both of these values are at best coarse estimators of male reproductive success. Plainly the extrusion of milt by itself does not guarantee the production of offspring. Multiple male spawnings occur and in general males that occupy satellite positions or that participate in spawnings that have already commenced, will fertilize fewer eggs than males that are closer in time and space to when and where eggs are deposited. Nonetheless such fish probably expend as much milt during a spawning as their more successful competitors. Thus any parameter based on presumed gonadal use may over estimate male reproductive success because not all releases of milt have equal probabilities of fertilizing eggs.

PGD and PRT values are based on the identical assumption that males allocate a consistent percentage of their body weight toward gonads. PGD values for instance, are produced by dividing the testes weight obtained from male at death by a testes weight that the male was predicted to have had at maturation. On a number of occasions we found that the weight of the testes we collected at death was greater than the one estimated for a male based on his body weight at maturity. When that occurred we obtained a negative PGD value. PRT values on the other hand, were simply calculated by dividing the testes weight observed at death by a male's weight at maturity. This seems to us to represent a more direct measure of male spawning participation. In the table below (Table 20) we show the results of regressions that examined the relationship between PRT and PGD values and actual reproductive success in the hatchery and wild males spawning in the observation stream. If a relationship exists between loss of male gonadal material and reproductive success the slopes of these regressions should be negative. Negative slopes occurred in all twelve regressions. Although not examined in a quantitative way, it appears that a stronger relationship between PRT and male RS occurred than existed between PGD and RS.

Table 20. The relationship between two measures of male spawning participation, PGD and PRT and reproductive success (RS) in hatchery and wild male spring chinook spawning in the observation stream in 2001. Arcsine transformed values of RS, PGD, and PRT were used in these analyses.

Upper Portion Of The Observation Stream				
Regression	n	Slope	F	P value
Hatchery Male PRT values vs. Male RS values	11	-0.3316	0.074	0.792
Wild Male PRT values vs. Male RS values	12	-3.045	9.113	0.013*
Hatchery- and Wild-Male PRT values vs. RS values	23	-1.963	6.149	.0217*
Hatchery Male PGD values vs. RS values	11	-.018	0.020	0.889
Wild Male PGD values vs. RS values	12	-0.344	6.080	0.033*
Hatchery- and Wild Male PGD values vs. RS values	23	-0.184	3.578	0.072
Lower Portion Of The Observation Stream				
Hatchery Male PRT values vs. Male RS values	7	-3.087	9.102	0.030*
Wild Male PRT values vs. Male RS values	10	-1.298	0.865	0.380
Hatchery- and Wild-Male PRT values vs. RS values	17	-2.189	7.017	0.018*
Hatchery Male PGD values vs. RS values	7	-0.411	5.461	0.067
Wild Male PGD values vs. RS values	10	-0.057	0.123	0.735
Hatchery- and Wild Male PGD values vs. RS values	17	-0.196	2.760	0.117

The probable reason for this is that both PGD and PRT percentages were arcsine transformed before being run in the analyses shown above. It is not possible to produce arcsine values on negative percentages. In those cases where negative values occurred we assumed that the males had not spawned at all and hence that no gonad depletion had occurred. Whenever this occurred an arcsine value of 90.00 was no matter what the value of the negative percentage might have been. This approach forced us to reduce the variation in this statistic and that may account for why it appears to be more weakly associated with male RS than PRT values. Correlation analyses were run on the PRT and PGD values obtained on the all the males placed into the upper and lower portions of the observation stream. The results of these tests showed these two random variables were almost perfectly correlated with one another (in the upper section $r = .98$, $n = 23$; in the lower section $r = .94$, $n = 17$). Consequently, we plan on only calculating and comparing

male PRT values in future analyses since it appears to provide a better indicator of male reproductive success than the alternative PGD value.

Predictors of spawning participation like PRT, PGD in males and percent spawned in females are simply estimators of reproductive success. In that in the past they were often the best indicators that researchers could use to develop inferences about the reproductive capabilities of the fish being examined. Having the power to actually identify the parental origins of the fry produced from the observation stream by using msDNA provides us with a means to unambiguously measure RS in hatchery and wild fish. Even though PRT and PGD values in wild and hatchery males were similar, the RS values showed that in the upper portion of the observation stream wild males were more successful at producing offspring than hatchery origin competitors. In the lower section, however, no difference in male RS due to treatment origin was discovered. The pedigree results originating from this section showed that some hatchery males were very successful at producing fry and these results appear to closely coincide with the behavioral observations we have analyzed so far on this population. Also, the msDNA based pedigree analyses allowed us to examine whether there was a proclivity for hatchery- or wild- origin males to preferentially spawn with wild or hatchery females. Such a tendency was not found. Both types of males appeared to fertilize eggs on the basis of simple opportunity.

Additionally, in 2000, and again in 2001 we had an opportunity to evaluate the reproductive success of precocious males via msDNA analyses. Prior to our study, no one that we are aware of has performed such an analysis. Our results demonstrate that these small males are able to successfully fertilize eggs in natural spawning situations. They clearly established dominance hierarchies among themselves and were very adept at deciphering cues broadcast by the larger spring chinook spawning in their portion of the observation stream. As noted in the results, they proved to be more successful than some jacks, and the larger 1+ hatchery precocious males clearly had greater RS values than the significantly smaller wild precocious fish that were placed into the observation stream. However, even wild precocious males that measured 70 to 80 mm and were 0+ fish managed to fertilize some eggs.

Adult spring chinook were certainly aware of their presence. For example, transcriptions of some of our behavioral observations noted that males often repeatedly chased and attempted to bite precocious males, as did the females that were being courted. Sometimes they were successful as several dead precocious males recovered from the observation stream had clear bite marks on their mid-bodies. Eventually, however, the larger anadromous adults either became habituated to their presence or no longer had the energy to expend on such chases. When that occurred, these fish remained next to spawning pairs and interacted among themselves, attempting to get in close proximity to the larger fish in an apparent effort to fertilize eggs. We saw a number of spawnings where these fish were in attendance. In none of these cases did any of them attempt to feed on newly extruded eggs. They appeared to be there to fertilize eggs and for no other purpose. We also performed post-mortem evaluations on these fish, and found that their

testes were often quite reduced in size and red, two indicators that the fish had spawned prior to dying.

The pedigree analyses also clearly showed distinctive differences in the capacity of each sex to produce off-spring. Some males apparently never spawned while others may have produced more than 7,000 offspring. A value that was more than twice as large as the most successful female. The behavioral observations we have so far analyzed indicate that a variety of behavioral attributes affect male RS values. Chief among these is their relative dominance over other competing males. Body size *per se* does not always determine which males achieve high dominance scores. Relative aggressiveness also plays an important role. A male that is passive, or easily dominated no matter what his relative size will produce few offspring. On the other hand, being too aggressive can be costly for if a male continuously chases potential rivals or engages in long chases he may loose out on fertilization opportunities that he might otherwise have been able to capitalize on. One of the most successful male strategies was to continuously attack any fish that was within 3 to 5 m of the female he was courting. Such a tactic created a cleared zone around a female and often allowed a male to spawn without the presence of other competitors in attendance. Female choice as exhibited by overt aggression also appeared to play a profound role in male RS. We found that males frequently chased or attacked by females had significantly lower RS scores than those that were not attacked by females.

We are in process of transcribing hours of audiotape that can be used to further describe the behavior of the fish while they spawned in the observation stream. These records will provide us with a more detailed understanding of any behavioral differences that might exist between hatchery and wild males and females. So far we have seen a number of differences in the reproductive performance of hatchery and wild fish. If these same differences are observed year after year then their effects will have to be considered whenever supplementation via hatchery intervention is being planned.

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